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Seasonal and spatial variability of soil respiration in four Sitka spruce stands

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Abstract We investigated the causes for the seasonal and spatial variation of soil respiration in a first rotation Sitka spruce chronosequence composed of four age classes (10, 15, 31, and 47 year old) in Central Ireland. The study aimed at identifying easily determinable environmental parameters that explained the variation in soil respiration rates. The variation in temperature and soil water content influenced the seasonal trend observed in the spatial variability of soil respiration. The highest coefficients of variation in soil respiration were observed during autumn drought, while lower coefficients were generally observed during periods with highest soil respiration rates. On average, the sampling strategy of 30 sampling points per stand was adequate to obtain an average rate of soil respiration within 20% of its actual value at the 95% confidence level. Significantly higher soil respiration rates were observed at locations with high accumulation of organic matter and in collars established in close vicinity to tree stems. The organic layer thickness was the only variable that yielded significant regressions for explaining spatial variation in soil respiration in all the stands. Correlation analyses between the studied variables and soil respiration suggested the relative importance of heterotrophic and autotrophic components differed in their annual contribution to total soil respiration at each forest stand. Multiple regression analyses were used to assess the relative importance of primary temporal and spatial controls over soil respiration. Soil temperature and organic layer thickness explained most of the variance of soil respiration for the different sampling periods, while soil water content had a weaker effect as well as a different influence on soil respiration depending on the time of the year. The strong linear correlation between forest floor carbon and soil carbon stock further confirmed organic layer thickness as an integrative factor encompassing the effect of soil carbon pools on soil respiration. Moreover, its inclusion in the multiple regression analyses overrode the influence of both distance and fine root biomass. Overall, a multiple linear regression model driven by easily determinable environmental variables such as soil temperature, organic thickness, soil water content, soil bulk density, and soil organic carbon concentration allowed us to explain 54% of total variance of soil respiration over the different stand ages for the entire year

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($P < 0.05$). Our results show that the adoption of an adequate sampling strategy, and the determination of some key environmental variables may help to explain a large proportion of total variation of soil respiration over the entire rotation length of afforested ecosystems.

Keywords Gley soil · Organic layer thickness · Seasonal variation · Soil respiration · Spatial variation · Sitka spruce chronosequence

Introduction

Over the past two decades, extensive research has been carried out on the factors influencing soil respiration in terrestrial ecosystems. In forests, total ecosystem respiration tends to be dominated by soil respiration, which accounts for approximately 69% of this large flux (Janssens et al. 2001). Soil respiration is primarily determined by the microbiological decay of organic matter and the respiration of living plant roots due to biochemical processes (Boone et al. 1998; Buchmann 2000; Hanson et al. 2000). Both decomposition of organic matter and root respiration have been found to be highly variable in space and time (Rochette et al. 1991; Longdoz et al. 2000; Rayment and Jarvis 2000; Stoyan et al. 2000).

Soil temperature and soil water content are recognised as the main factors controlling the temporal variability of soil respiration (Davidson et al. 1998; Longdoz et al. 2000; Janssens et al. 2001). Confounding effects of drought and high water content on the sensitivity of soil respiration to temperature have been reported (Davidson et al. 1998; Curiel Yuste et al. 2003). Additionally, the seasonal variation of soil respiration is strongly influenced by plant photosynthetic activity (Högberg et al. 2001; Kuzyakov and Cheng 2001; Bhupinderpal-Singh et al. 2003). On an annual scale, the temporal variability that goes unaccounted for with the use of regressions based on climatic variables may be due to seasonal variability in the microbial, root and litter biomass (Longdoz et al. 2000). However, the importance of these biotic variables on the temporal variation of soil respiration will be dependant on the type of forest ecosystem being studied (Kang et al. 2003).

Spatial heterogeneity in soil CO_2 efflux rates is large, even in what appear to be relatively homogeneous stands (Raich et al. 1990). The spatial variability of soil respiration rates is affected by the spatial distribution of fine roots. Several studies show a significant positive relationship between fine root biomass and soil respiration (Pregitzer et al. 2000; Widén and Majdi 2001; Saiz et al. 2006). Roots not only make a direct contribution to the total soil CO_2 efflux, they also affect the respiratory activity of heterotrophic organisms via exudation of carbon-rich substances and by altering the soil physical and chemical environment (Kuzyakov and Cheng 2001). Other factors controlling soil respiration are e.g. texture, total soil organic carbon, and distribution of organic matter, which are all affected by topography (Fang et al. 1998). Rout and Gupta (1989) as well as Klopatek (2002) have shown that the spatial variability of soil respiration is driven by the mass of litter accumulation on the forest floor, and different qualities and quantities of soil carbon pools.

To study the spatial variation of soil respiration one can make use of portable soil respiration systems allowing sampling over many locations, thus increasing the confidence in the site mean estimate of soil respiration with respect to spatial heterogeneity (Savage and Davidson 2003). The use of a stratified sampling design that reflects variation in the spatial pattern can significantly reduce the number of samples required to estimate mean soil respiration rates (Rochette et al. 1991; Fang et al. 1998; E.S.F. 2000). Moreover, a stratified random sampling design, with sampling points stratified according to distance to the nearest tree may yield more reliable estimates of greenhouse gas emissions from a given stand (Butterbach-Bahl et al. 2002). Such sampling strategy has also been shown to be a more accurate method for determining fine root density than systematic sampling designs (Olsthoorn et al. 1999). The need for a stratified sampling design for estimating soil respiration at the stand level is further supported by findings by Wiseman and Seiler (2004). These authors reported higher soil respiration rates close to tree stems.

We conducted a study on a first rotation Sitka spruce (*Picea sitchensis* (Bong.) Carr.)

chronosequence composed of four age classes (10, 15, 31, and 47 year old) in Central Ireland. The objectives of the study were: (1) to investigate the seasonal and spatial variation of soil respiration and to determine the number of sampling points required to estimate mean soil respiration within a given confidence level at each site, and (2) to identify easily determinable environmental parameters that explained the temporal and spatial variance in soil respiration.

Materials and methods

Sites description

The forest stands investigated were Sitka spruce (*Picea sitchensis* (Bong.) Carr.) first rotation plantations established on former grassland (afforestation sites). The study sites were located at the Dooary forest (52°57′ N, 7°15′ W) in the Irish midlands at an elevation of 260 m. Long term mean annual temperature and average annual precipitation for the region are 9.3°C and 804 mm, respectively (Met Eireann, Irish Meteorological Service).

The study was carried out on 10, 15, 31 and 47 year old stands, with the oldest stand being mature for harvest. The selected sites were within 5 km of each other. A number of regular thinnings (3–4) had already taken place in 31 and 47 year old plantations. All the stands in the present study had reached canopy closure and were characterised by a nearly absolute absence of understory or herbaceous vegetation. Neither fertilisation nor drainage works were carried out since tree establishment in any of the stands (Coillte Teoranta, the Irish Forestry Board, personal communication).

The 10 and 15 year old stands had been established along ripped lines 1 m deep and 2 m apart. Surface drains across the ripped lines had been made at 50 m intervals. In the case of the 31 and 47 year old stands, these sites were ploughed at 1.7 m intervals following the contour lines of the slope. At the plot level, these operations prior to tree establishment created a series of topographical variations in the form of ridges, furrows, and undisturbed ground which promoted the presence of areas with varying degrees of forest floor (organic layer) coverage. Soil types were classified as low humic (mineral) gleys in the 10, 15, and 31 year old stands, and as gleyic brown earth in the 47 year old stand which seemed to have appreciably better drainage due to its location on sloping terrain. Soils presented low pH values (<4.8) at all sites. Soil nitrogen concentration ranged from 0.63 to 0.42% observed in the 10 and 15 year old sites, respectively. Similarly, phosphorous content across all sites was within a limited range of values 11.4–8.8 ppm. For a more detailed description of the sites and tree characteristics of the chronosequence see Saiz et al. (2006).

Experimental design and measurement of environmental factors

At each forest stand, a stratified random sampling design for the measurement of soil respiration was put in place on the basis of both the degree of disturbance made to the soil when the trees were established and distance from the closest tree stem. Trees were randomly chosen from within 30×30 m plots. The study plots were randomly placed, and they were at least 20 m from stand discontinuities or its boundaries. A series of 30 PVC circular collars (16 cm i.d.) per stand were inserted into the soil to an average depth of 1.5 cm for measurements of total soil respiration. Collars set at this depth were stable and caused minimal disturbance to shallow fine roots. Collars were proportionally distributed to the area occupied by furrows, ridges and undisturbed ground to account for morphologically driven differences in soil respiration. Soil respiration collars were set up at fixed distances (i.e. 15, 30, 45, 60, 90, and 120 cm) from the nearest tree stem at the furrows, ridges, and undisturbed ground. Areas closer to the tree stem were more intensively sampled because preliminary studies had shown higher variability in soil respiration at those locations.

Soil respiration was measured using a portable infrared gas analyser connected to a soil respiration chamber having a headspace volume of 2250 cm^3 (EGM-4 and modified SRC-1; PP Systems, Hitchin, U.K.). The chamber was fitted with a rubber-foamed ring cemented to a modified lip

to ensure a tight seal with the soil collars. The measuring principle is a closed system that determines the increase in CO_2 concentration within the chamber over time. The rate of increase was expected to be linear over a period of 2 min or a built-in system device warned of excessive non-linearity. The latter indicated a likely gas leakage; in such a case the reading was discarded. An internal fan assured a homogeneous mixture of the chamber's air. The system was calibrated before each sampling day against CO_2 with a nominal concentration of 409 ppmv.

Soil respiration measurements were carried out during 2003 at all sites on a monthly basis to account for seasonal variability of soil respiration. Measurements were made between 10 a.m. and 4 p.m. While the importance of diel variation in soil CO_2 efflux has been recognised in agricultural research (Parkin and Kaspari 2003), this variation is less important in heavily shaded forested areas (Epron et al. 1999; Davidson et al. 2000).

The number of samplings required to estimate the mean soil respiration of each stand at the 10 or 20% of its actual value at the 95% probability level was obtained using the relationship described by Snedecor and Cochran (1967);

$$n = \left(\frac{t_\alpha s}{D}\right)^2$$

where t_α is Student's t with degrees of freedom at the 0.05 probability level, s is the standard deviation with values obtained at this study, and D is the specified error limit. The 30 measurements per sampling day were tested for normality prior to these calculations.

Soil temperature at different depths was measured adjacent to each collar (220 K temperature meter, Jenway, Essex, U.K.). The probe was sequentially inserted into soil depths of 2, 6 and 10 cm. Soil water content within every collar was determined using a moisture probe (ThetaProbe ML2x, Delta-T Devices, Cambridge, U.K.).

At the end of the study all locations for soil respiration were sampled for assessing the thickness of the organic layer. Similarly, the mineral soil was sampled by horizon up to a depth of 30 cm for determining both soil organic carbon and soil bulk density. These soil samplings were conducted at 5–8 locations per topographic feature (furrow, ridge, and undisturbed ground), resulting in 15 sampling locations per site being studied. The samples were taken to the laboratory, where they were air dried and sieved through a 2 mm sieve. The organic matter in the soil samples was determined using the loss on ignition technique (Ben-Dor and Banin 1989). To validate our method for estimation of soil organic matter, a number of sub samples were also analysed by the Walkley–Black wet oxidation technique. A relationship between organic matter and loss on ignition was developed and used to estimate organic matter for the entire loss on ignition sample set (Green, unpublished data). Soil bulk density was determined using the volumetric core method (Blake and Hartge 1986). Undisturbed cores from the top-soil horizon were collected with the aid of an 8 cm diameter corer following the same sampling strategy used for soil organic carbon and soil bulk density determination. The samples were then oven dried at 105°C until constant weight to determine soil bulk density.

For determination of fine root biomass, between 7 and 15 soil cores per site were retrieved with the aid of a root auger (8 cm diameter) up to a depth of 30 cm. Samples were immediately stored at 4°C until they were further processed in the laboratory. The organic layer and the different soil horizons were separated. All samples were then rinsed and sieved to detach fine roots from soil mineral particles. This analysis was carried out within four days of the samples being collected. Roots were sorted into three diameter classes (<1, 1–2 and 2–5 mm). Finally, washed roots were weighed after being oven-dried at 70°C for 48 h to determine fine root biomass.

Statistical analysis

Data sets were tested for normal distribution by the Kolmogorov–Smirnov test. We used SigmaPlot 8.0 to smooth our data to a rectangular grid of independent variable values in order to observe the response of soil respiration rates to changes in soil temperature and soil moisture. A tricube weight function $\left(1 - |u|^3\right)^3$ was applied to weight the data. The weight assigned to each

data value was determined by its normalised distance (u) from the smoothing location. A polynomial of degree one was then applied to the weighted data to compute each smoothed value.

Within the same stand age class, a one-way ANOVA was performed to compare soil respiration rates, organic layer thickness, soil organic carbon concentration, and soil bulk density between different locations. Soil temperature and soil water content among the different stands were also compared using the same statistical approach. Correlation analyses were used to examine relationships between soil respiration rates and the different variables. Variables such as soil nitrogen, phosphorous, and pH were not determined at each sampling location, and consequently were not included in the analyses. Multiple regression analyses were performed using the stepwise procedure in SPSS (SPSS 12.0 Inc., Chicago, IL, USA) at the $P = 0.05$ significance level.

Results

Seasonal variation of soil respiration

No significant differences in mean annual soil temperature were found between the stands ($P > 0.05$). Soil volumetric water contents showed no significant differences among three of the four stands over the course of the year ($P > 0.05$). The 31 year old stand had a lower soil water content compared to the rest of the stands. Soil respiration experienced a distinct seasonal variation that paralleled the seasonality observed in soil temperature. The lowest soil respiration rate observed during winter was 24 ± 10.9 mg C m^{-2} h^{-1} occurring at the oldest stand. By contrast, values of soil respiration peaked in late July or early August in all the stands, being the maximum rate of 220 ± 73.6 mg C m^{-2} h^{-1} observed at the youngest stand (Table 1). Subsequently, soil respiration rates followed a steady decrease towards the end of the year, with the exception of sites where soil water content rates dropped to values below 20% between late summer and mid autumn. In such cases, there was an abrupt drop in soil respiration, which reached a rate as low as 16 ± 13.6 mg C m^{-2} h^{-1} at the 31 year old stand.

Table 1 Number of sampling points required per sampling date to estimate mean soil respiration within 10 or 20% of its actual value at the 95% probability level for each stand age

Day of the Year	10 year old				15 year old				31 year old				47 year old			
	Soil Resp.	SD	*N*-10%	*N*-20%	Soil Resp.	SD	*N*-10%	*N*-20%	Soil Resp.	SD	*N*-10%	*N*-20%	Soil Resp.	SD	*N*-10%	*N*-20%
21	54.6	16.4	38	9	35.5	19.1	121	30	51.8	27.3	116	29	24.5	10.9	83	21
40	49.1	16.4	46	12	54.5	24.5	85	21	30.0	19.1	169	42	24.5	13.6	129	32
85	111.8	21.8	16	4	68.2	35.5	113	28	49.1	19.1	63	16	43.6	19.1	80	20
135	125.4	18.1	9	2	100.9	30.0	37	9	79.1	40.8	111	28	84.5	27.3	44	11
168	147.3	40.9	32	8	76.4	30.0	65	16	95.4	38.2	67	17	87.3	38.2	80	20
211	220.9	73.6	46	12	139.1	49.1	52	13	133.6	32.7	25	6	125.4	27.3	20	5
225	217.3	82.6	60	15	163.6	51.8	42	10	106.4	54.6	110	27	111.0	42.2	60	15
247	144.5	60.0	72	18	84.5	62.7	230	58	76.4	68.2	333	83	79.1	35.5	84	21
289	92.7	43.6	93	23	87.3	21.8	26	7	16.4	13.6	290	73	84.5	40.9	98	24
317	100.9	38.2	60	15	70.9	51.8	223	56	68.2	49.1	217	54	65.4	27.3	73	18
351	65.4	16.4	26	7	35.4	16.4	89	22	51.8	21.8	74	19	45.0	13.5	38	9
Average number of points req.			45	11			98	25			143	36			72	18

Mean soil respiration rates and standard deviations (mg C m^{-2} h^{-1})

This last figure was the absolute minimum rate for all the stands, including winter time.

Temporal trends in the spatial variability of soil respiration

The spatial variability of soil respiration can be described by the coefficient of variation (CV) of each series of measurements. The CVs ranged from a minimum value of 14% calculated for the 10 year old stand to a maximum value of 90% calculated for the 31 year old stand (Fig. 1a). There was a seasonal trend in the spatial variability of soil respiration, with the highest CV occurring during autumn at a time of high temperatures and low soil water contents, except for the case of the 47 year old stand whose highest CV was observed in winter. On the other hand, the lowest CV values were generally observed coincidentally with annual highest soil respiration rates. Figure 1b focuses on the 31 year old stand and the evolution in the CV of both soil

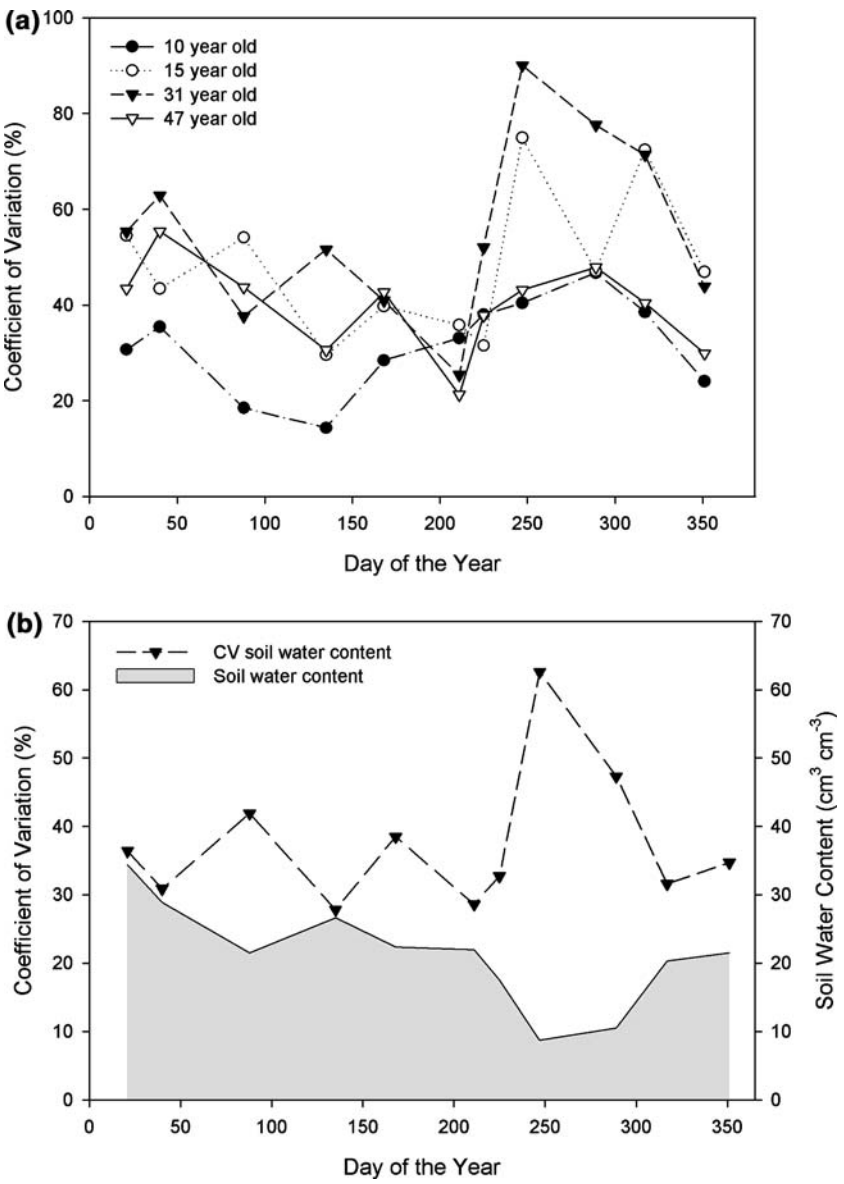

Fig. 1 (**a**) Seasonal evolution of the coefficients of variation of soil respiration for the different sites; (**b**) Seasonal evolution of the coefficient of variation of soil water content, and variations in soil water content for the 31 year old stand

respiration and soil water content. The spatial variability of soil water content sharply increases when soil water content falls well below 20%, and the resultant CV of soil respiration reaches its maximum during this period (Fig. 1a).

The number of measurements required to estimate soil respiration per stand and sampling date within 10 or 20% of its actual value at the 0.05 probability level, are shown in Table 1. On average, our sampling strategy of 30 sampling points per stand was adequate to obtain an average rate of soil respiration within 20% of its actual value at any sampling date. However, the 31 year old stand was the most affected by drought-related limitations in soil respiration. To accurately determine its respiration rate within the confidence intervals previously described during drought events in late summer >300 or >80 measurements would be necessary at the 10% and 20% accuracy, respectively (Table 1).

Spatial variation of soil respiration

For each forest stand, significantly higher soil respiration rates were generally obtained in collars placed on furrows (if present) compared to the ones measured at ridges or undisturbed ground that showed no significant differences between them (Table 2). Furrows had significantly higher organic layer thickness than either the ridges or the undisturbed grounds that showed no significant differences between them (Table 2). Analyses of soil organic carbon concentration showed no significant differences between the different topographical features (Table 2). Differences in bulk density could not be demonstrated either.

Simple regression analyses were carried out to investigate the relationships between possible driving variables and within site variability of soil respiration at each forest stand. Consistently for all sites, the best single factor explaining the collar-to-collar variation of soil respiration was the thickness of the organic layer (Table 3). The inclusion of other variables (i.e. soil organic carbon, bulk density, etc) provided non-significant models that made little improvement on the predictability of the spatial variation of the flux.

Table 2 Soil respiration rates and parameters relevant for the different topographical features of the different stands that compose the chronosequence

	10 year old		15 year old		31 year old			47 year old		
	Undisturbed ground	Ridges	Undisturbed ground	Ridges	Undisturbed ground	Ridges	Furrows	Undisturbed ground	Ridges	Furrows
Soil CO_2 efflux (mg C m^{-2} h^{-1})	151.5 ± 9.8^{a}	140.4 ± 10.9^{a}	98.9 ± 5.3^{a}	106.1 ± 12.8^{a}	80.6 ± 7.6^{a}	88.6 ± 10.5^{a}	114.8 ± 13.7^{b}	80.1 ± 9.1^{ab}	66.4 ± 12.3^{a}	109.5 ± 10.2^{b}
OL thickness (cm)	4.2 ± 0.3^{a}	3.9 ± 0.3^{a}	3.9 ± 0.2^{a}	4.5 ± 0.3^{a}	3.0 ± 0.3^{a}	3.0 ± 0.6^{a}	3.9 ± 0.3^{b}	2.3 ± 0.2^{a}	1.9 ± 0.4^{a}	3.1 ± 0.1^{b}
Mineral layer carbon conc. (%)	7.42 ± 0.47^{a}	6.44 ± 0.52^{a}	4.86 ± 0.46^{a}	4.36 ± 0.61^{a}	7.06 ± 0.62^{a}	6.97 ± 0.42^{a}	7.28 ± 1.06^{a}	6.47 ± 0.98^{a}	6.89 ± 0.95^{a}	7.30 ± 1.51^{a}
Mineral layer bulk density (g cm^{-3})	0.70 ± 0.03^{a}	0.70 ± 0.01^{a}	0.83 ± 0.01^{a}	0.88 ± 0.06^{a}	0.86 ± 0.04^{a}	0.77 ± 0.02^{a}	0.80 ± 0.08^{a}	0.82 ± 0.03^{a}	0.81 ± 0.05^{a}	0.80 ± 0.06^{a}

Number of samples per stand age was 30 for soil respiration, 30 for organic layer (OL) thickness, and 15 for mineral soil carbon concentration and soil bulk density. Samples were randomly and proportionally distributed between the strata (topographical features). Mineral soil parameters are presented for A_1 horizon (8–10 cm thickness). Different letters along the rows within the same age stands denote significantly different rates ($P < 0.05$); ANOVA, Tukey post hoc test

Table 3 Summary of the regression analyses carried out to investigate the causes of within site spatial variability of soil respiration

Sites	Model	r^2	F	df	P
10 year old	SR = 24.46 + 47.33 OL	0.54	36.80	29	0.000
15 year old	SR = 40.60 + 15.47 OL	0.19	5.06	29	0.035
31 year old	SR = 19.44 + 23.85 OL	0.48	21.88	29	0.000
47 year old	SR = –9.89 + 38.97 OL	0.60	27.42	29	0.000
All stand ages	SR = 21.85 + 25.59 OL	0.49	95.64	119	0.000

(SR): Soil respiration (mg C m^{-2} h^{-1}); (OL): Organic layer thickness (cm). Regressions significant at $P < 0.05$ level are shown

Correlations of biotic and abiotic variables with soil respiration

Soil respiration was highly correlated with soil temperature in all the stands of the chronosequence, with r values ranging from 0.64 to 0.44, $P < 0.01$ (Fig. 2a). Considering all the stands together, soil water content was positively correlated to soil respiration during the growing season, while this correlation was negative but not significant during the non-growing season (Fig. 2b). On the other hand, there was a significant negative autocorrelation between soil temperature and soil water content, but the degree of correlation was low ($r > –0.2$ for any period).

A combined effect of both soil temperature and water content on soil respiration is shown in Fig. 3. During the non-growing season low soil respiration rates were observed due to low soil temperatures. In addition to low soil temperatures, high soil water content further reduced soil respiration during the non-growing season. However, with increasing soil temperatures, the effect of high soil water content enhanced soil respiration (Fig. 3). The stand specific differences observed in Fig. 3 show that the response of soil respiration to variations in temperature and moisture was most obvious for the youngest stands. Similarly, the amplitude in soil respiration was highest for these youngest stands. The previously described limitation in soil respiration by seasonal drought was most obvious in the 31 year old stand as a result of both its topography and orientation.

Organic layer thickness was highly correlated with soil respiration at all stands (Fig. 2a). The strong positive relationship between soil respiration and the organic thickness was also supported by the fact that a large proportion of total fine root biomass present in the soil profile was concentrated at this most superficial layer (Fig. 4). For all stand ages, over 50% of the total fine root biomass (<1 mm diameter) present in the soil profile (to 30 cm depth) were observed in the organic layer, with the only exception of the 47 year old stand, where the proportion of fine roots in the organic layer was only 34%. There was a strong negative relationship between soil respiration and the distance from the nearest tree stem in all the stand ages, i.e. soil respiration was highest close to the stem. The only case in which such a relationship was not significant was in the most mature stand (47 year old). Figure 5 shows the significant decrease of soil respiration with increasing distance from the base of the closes tree. Organic carbon concentration in the mineral layers was significantly correlated with soil respiration at the 47 year old stand only (Fig. 2a). Bulk density in the mineral soil layer was negatively correlated to soil respiration, although such relationships were not significant. Similarly, fine root biomass alone did not show any significant relationship with soil respiration, except for the case of the youngest stand $P < 0.05$ (Fig. 2a).

Variance in total seasonal and spatial soil respiration

Multiple regression analyses were carried out using pooled data from all the stands over the entire year, and between growing and non-growing periods with the objective of identifying which variables best explained the variation in seasonal and spatial soil respiration over these two distinctive periods. A stepwise procedure was used to

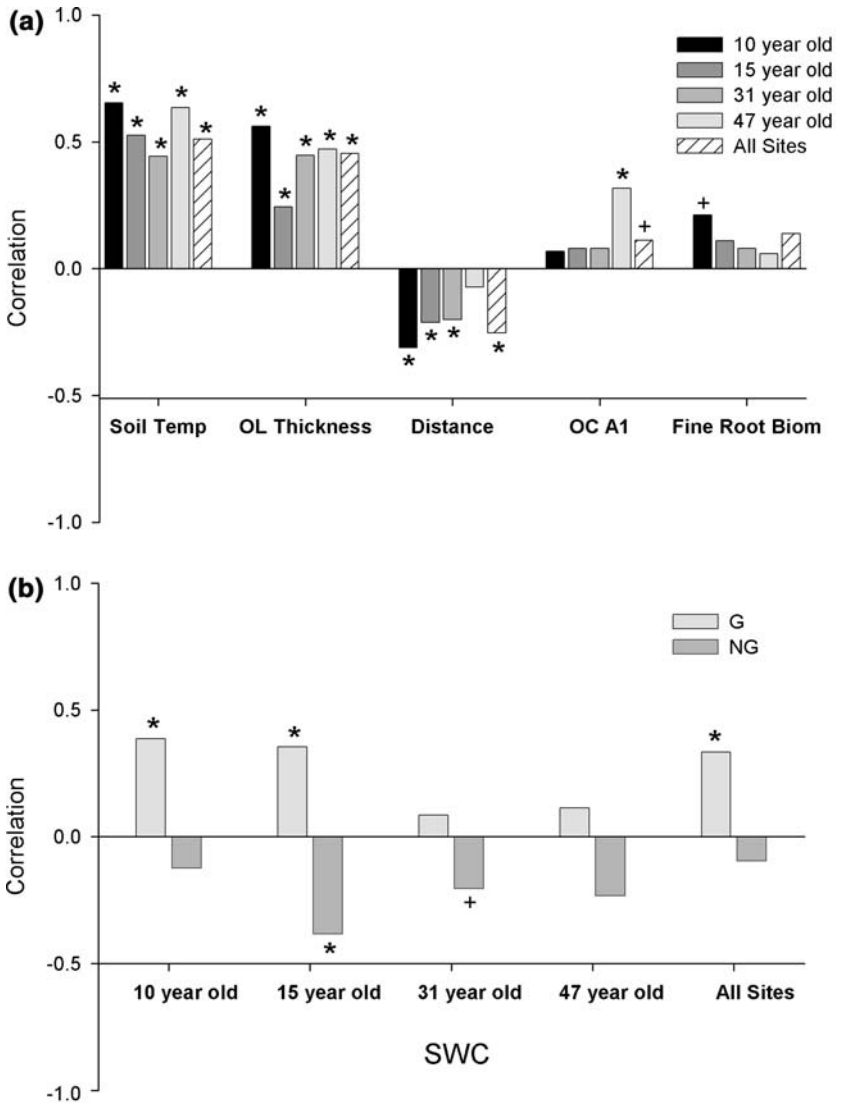

Fig. 2 (**a**) Correlation analyses between soil respiration and soil temperature, organic layer thickness, distance from the tree stem, organic carbon concentration in the A_1 horizon, and fine root biomass for the different stands; (**b**) Correlation analyses between soil respiration and soil water content (SWC) separated by G (growing) and NG (non-growing) seasons for the different stands. Correlation values are Pearson's coefficients. Asterisk and cross symbols denote significant correlations at the $P < 0.01$ and $P < 0.05$ level, respectively

reduce the number of parameters and use only those that were significant at the 0.05 level. Following the analyses, selected variables were soil temperature, organic layer thickness, bulk density from the top mineral layer, soil water content, and organic carbon concentration measured in the top mineral layer. The discarded variables were either not significant in the analyses or were highly autocorrelated with other variables. Cumulative fits and regression coefficients for the different variables are presented in Table 4. Soil temperature and organic layer thickness explained most of the variation of soil respiration for the different sampling periods. These two parameters alone could explain up to 46% of annual and spatial variation of soil respiratory flux (Table 4). Bulk density in the top mineral layer contributed 6% further in explaining total variability of soil respiration. Soil water content had a negative though very limited influence in soil respiration during the non-growing season. However, it had the opposite effect during the growing season. The latter was proved by the contrasting coefficients obtained in the multiple regression analyses for the non-growing and growing season (Table 4). Organic carbon concentration had a positive effect on soil respiration although it did not improve substantially the estimates.

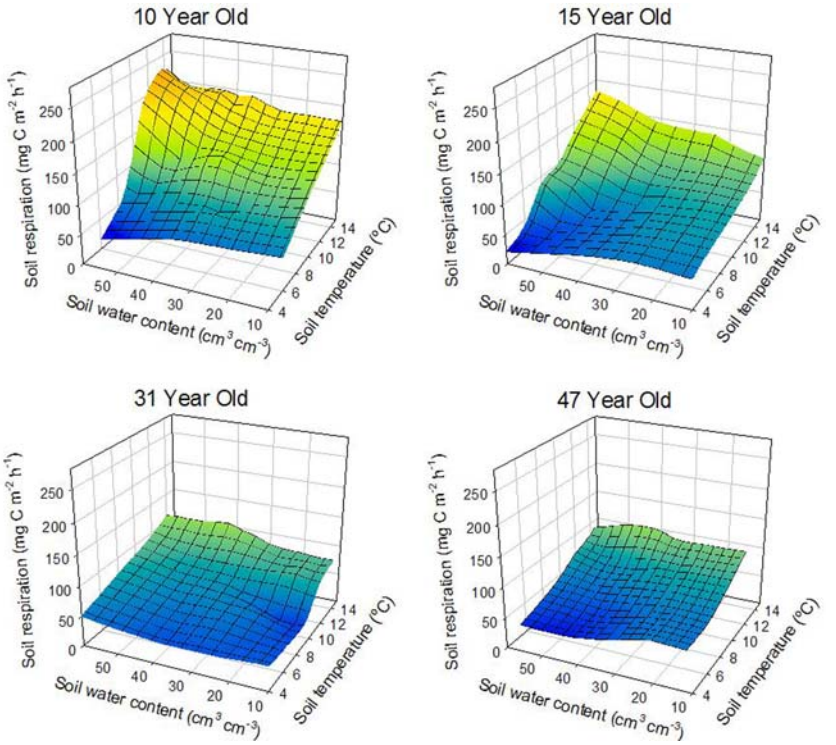

Fig. 3 Combined effect of soil temperature and water content on soil respiration for each specific stand. A description on the data smoothing is given in the statistical analyses section

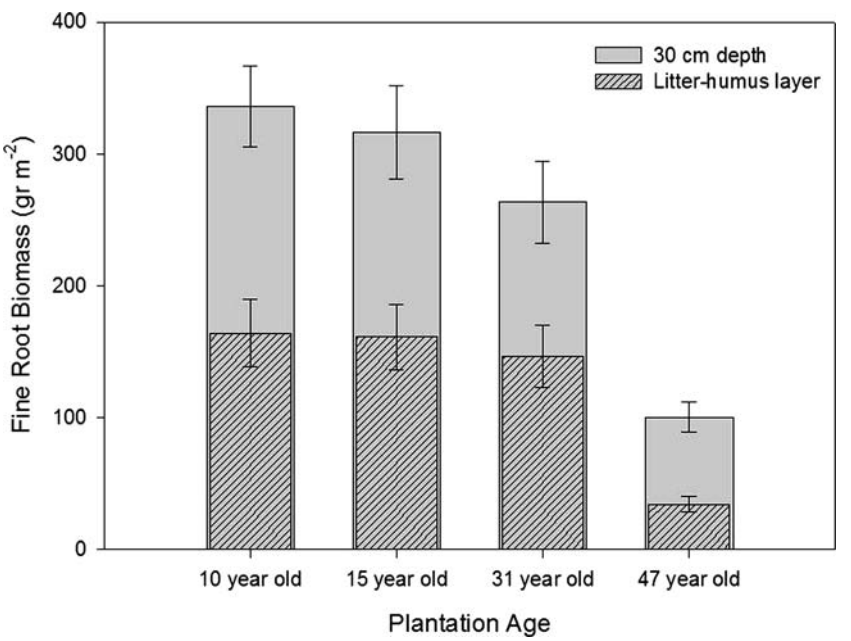

Fig. 4 Fine root biomass distribution along the soil profile for the different stand ages. Fine roots <1 mm diameter. The 47 year old stand has significantly lower fine root biomass in both the entire soil profile and the litter-humus layer ($P < 0.05$)

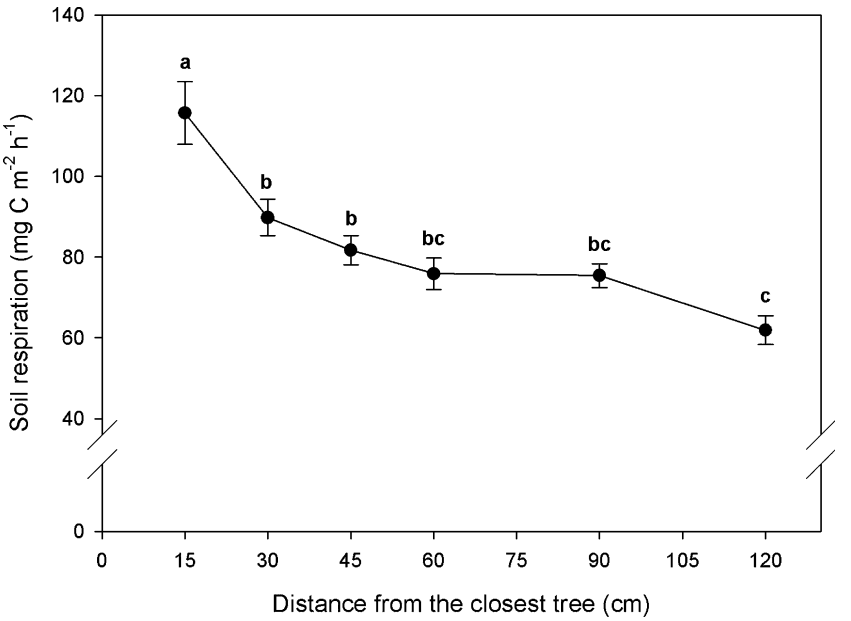

Fig. 5 Average soil respiration rates (mg C m^{-2} h^{-1}) at varying distances from the base of the closest tree. Mean values are based on sampling points measured at fixed distances from all stands (n = 1129). Error bars are standard errors of the means. Different letters denote significantly different soil respiration rates; ANOVA, Tukey post hoc test ($P < 0.05$)

Discussion

Seasonal pattern of spatial variability in soil respiration

The variation in temperature and soil water content influenced the seasonal trend observed in the spatial variability of soil respiration (Fig. 1). The limitation in soil respiration observed at a time of high soil temperatures may be attributed to drought stress on microbial communities and root activities (Epron et al. 1999; Rey et al. 2002). Therefore, metabolic activities will be more or less favoured depending on the specific environmental conditions present at a particular location. While soil temperature normally shows little spatial variation at a given time under conditions of canopy closure, this may not be the case with soil moisture. The presence of pockets or aggregates within the soil with higher water content than neighbouring areas is a normal feature, which may get more significant as the soil dries (Stoyan et al. 2000). This may partially explain the large differences in soil respiration rates between the collars and consequently the highest coefficients of variation obtained during autumn drought (Fig. 1b). The seasonal trend observed in the spatial variability of soil respiration agrees well with the shift in emissions from random heterotrophic hot spots to a more uniform spatial pattern in soil CO_2 emissions resulting from the presence of actively growing roots as reported in other research works (Rochette et al. 1991; Russell and Voroney 1998). Similarly, and in the context of the present study, the largest contributions of root respiration to total soil respiration were observed during the summer at all stand ages (Saiz et al. 2006), and coincidentally with both the highest observed soil respiration rates and lowest CV of soil respiration (Table 1, Fig. 1a; days of the year 211–225). Additionally, the spatial patterns in soil respiration may fluctuate during the season in response to other factors such as changes in organic matter inputs and microbial activities (Buchmann 2000; Stoyan et al. 2000).

The seasonal pattern of spatial variability in soil respiration can also be expressed by the number of measurements required to estimate soil respiration within a giving percentage of its actual value (Rochette et al. 1991). While the use of 30 sampling points per stand yielded an average rate of soil respiration within 20% of its actual value at any sampling date, the stands more affected by autumn drought events required a larger number of measurements during that

Table 4 Multiple regression analyses performed pooling all the stand ages for the different periods

Parameter	Non-growing season				Growing season				All year			
	Cumulative r^2	Coefficient	Error	P	Cumulative r^2	Coefficient	Error	P	Cumulative r^2	Coefficient	Error	P
Constant		149.554 (a)	22.911	0.000		87.395 (a)	32.412	0.007		16.273 (a)	37.231	0.662
T2	0.182	3.950 (b)	0.495	0.000	0.308	12.783 (b)	1.364	0.000	0.273	9.121 (b)	0.441	0.000
OL Thickness	0.338	11.034 (c)	1.101	0.000	0.429	24.159 (c)	1.531	0.000	0.460	20.055 (c)	1.198	0.000
BD A1	0.418	–191.18 (d)	25.174	0.000	0.516	–309.772 (d)	33.077	0.000	0.519	–180.012 (d)	31.200	0.000
SWC	0.426	–0.277 (e)	0.121	0.023	0.571	0.953 (e)	0.126	0.000	0.536	0.637 (e)	0.104	0.000
OC A1									0.540	0.461 (f)	0.177	0.009

All parameters and regressions are significant at $P = 0.05$ level, except for the constant parameter in the all year model. Degrees of freedom are 299, 359, and 659 for non-growing season, growing season, and all year polynomial models, respectively. Presented coefficients and their associated standard errors and P values make reference to the model showing the highest fit in each period

Soil Respiration (mg C m^{-2} h^{-1}); (T_2) Soil temperature at 2 cm (°C); (OL) Organic layer thickness (cm); (BD) Bulk density in the A_1 horizon (g cm^{-3}); (SWC) Soil water content (cm^3 cm^{-3}); (OC) Organic carbon in the A_1 horizon (g C cm^{-2})

Form of equation: Soil Respiration = a + T_2*b + OL Thickness*c + BD A_1*d + SWC*e + OC A_1*f

period (Table 1). However, drought during late summer and autumn 2003 was singular in Ireland as well as in the rest of Europe. Rainfall recorded for that period was around 20% lower compared to long term average values.

The comparison of the coefficients of variation between different studies is not helpful due to the lack of a standard design of experiments, and the disparity in the number of sampling positions and their arrangement (Fang et al. 1998). Furthermore, the number of measurements needed is also influenced by the area covered by the chamber (Davidson et al. 2002). Raich et al. (1990) pointed out that the use of an adequate sample size was more relevant to soil respiration than possible biases between the methods used for its determination.

Temporal variability of soil respiration

The main variable driving the temporal variation of soil CO_2 efflux among all the sites studied was soil temperature. The observed high correlation of soil temperature with soil respiration (Fig. 2a), is also a feature widely reported in previous studies (Raich and Schlesinger 1992; Fang et al. 1998; Buchmann 2000). Temperature based models calculated for these forest sites using mean monthly soil respiration rates explained up to 79% of the annual variation in soil respiration (Saiz et al. 2006). The effect of soil water content on soil respiration was quite different depending on the time of the year (Figs. 2b, 3). Water content was only stimulating for soil respiration during the growing season. Conversely, the reported confounding effect of high soil water content on soil respiration at low temperatures (Davidson et al. 1998), was also observed in our study as it is shown by the negative correlation between soil respiration and soil water content during the non-growing season (Fig. 2b). High soil water contents may limit soil respiration by limiting oxygen availability for both microbial decomposition and autotrophic activities (Davidson et al. 1998; Xu and Qi 2001; Rey et al. 2002). Kiese and Butterbach-Bahl (2002) observed that the varying soil water contents over two distinctive growing periods had the same effect in soil CO_2 fluxes as those reported in the present study.

Spatial variability of soil respiration

The existence of spatial patterns for variables governing soil processes may induce a similar spatial pattern of variability for soil respiration. The significantly higher respiration rates obtained in collars placed on furrows justified our stratified sampling design. The action of wind, and more importantly of water runoff, promoted the accumulation of litter and organic debris at these depressed locations (Table 2). While other factors affecting soil respiration such as bulk density and organic carbon concentration in the top mineral layer did not show significant differences between undisturbed ground, ridges or furrows, the presence of a thicker organic layer had a significant positive impact on the higher respiration rates observed at the furrows (Table 2). In fact, when regression analyses were performed at each forest stand to determine the causes of spatial variation in soil respiration, organic layer thickness was the only variable that yielded significant regressions (Table 3). The inability of temperature to explain the spatial variation of soil respiration was in accordance with other studies (Fang et al. 1998; Xu and Qi 2001; Scott-Denton et al. 2003). Soil water content has been shown either as a significant factor regulating spatial variability (Kang et al. 2003), or as not having such influence (Xu and Qi 2001; this issue). The remaining unexplained spatial variation may be due to both differences in microbial biomass and other soil physical and chemical properties, which were not determined at measurement location scale, and that may influence mineralisation and root activity.

The spatial variability of soil respiration has been reported to be linearly related to the thickness of the organic layer (Rayment and Jarvis 2000). A strong linear correlation between forest floor carbon and soil carbon stock was observed at these sites ($r^2 = 0.95$) (Green, unpublished data). Furthermore, work carried out by Scott-Denton et al. (2003) figured out the importance of the organic layer thickness as an integrative factor capable of subsuming the effect of soil carbon pools and accurately predicting spatial variance in soil respiration rates. This is in agreement with the strong positive relationship between soil respiration and the organic layer thickness obtained in our study (Fig. 2a), and with the fact that a large proportion of total fine root biomass present in the soil profile was concentrated in the organic layers (Fig. 4).

The negative correlation observed between soil respiration and tree distance obtained at all sites (Fig. 2a) has also been previously reported in several studies (Ben-Asher et al. 1994; Stoyan et al. 2000; Wiseman and Seiler 2004). Significantly higher soil respiration rates were obtained from collars established in close vicinity to tree stems (Fig. 5), which is most likely due to both the presence of a higher accumulation of organic matter near the base of the trees (see Butterbach-Bahl et al. 2002), and the higher concentration of fine root biomass present at these locations (data not shown). The distribution of the throughfall water, with the subsequent horizontal heterogeneity of soil water content and the chemical condition of the soil have potential influence on the fine root density in relation to tree positions (Olsthoorn et al. 1999). Furthermore, the spatial pattern of throughfall in Sitka spruce has been shown to parallel the distribution of fine roots, which results in the presence of a higher concentration of fine roots close to the tree stem (Ford and Deans 1978). We observed such a trend in our study, although our fine root biomass sampling intensity was not sufficient to perform any rigorous attempt to detect significant variations in fine root distribution.

Interestingly, the only case in which the negative relationship between soil respiration and distance from the closest tree stem was not significant was in the most mature stand (47 year old) (Fig. 2a), which compares well with findings by Wiseman and Seiler (2004). These authors found that the contribution of fine root respiration to total root respiration is likely similar near the tree and away from the tree at rotational maturity. On the other hand, the 47 year old stand showed the only significant correlation between organic carbon concentration in the mineral layer and soil respiration across all sites (Fig. 2a). The latter facts, together with the significantly lower fine root biomass observed at this site (Fig. 4), suggest that the microbial decomposition component at the 47 year old stand could contribute more to total soil respiration than in any of the other sites.

This is in good agreement with previous research work conducted at this chronosequence, which has shown that the lowest contribution of autotrophic respiration to total CO_2 efflux occurred in the 47 year old stand (49.7%), while this contribution was 59.3, 56.7, and 56.8% for the 10, 15, and 31 year old stands, respectively (Saiz et al. 2006). Furthermore, the same study revealed that compared to the younger stands, the lower autotrophic respiration observed at the 47 year old stand was compensated by a higher microbial decomposition activity due to the accumulation of organic matter inputs over the years, mostly in the organic layer and upper soil horizons.

Variance in total seasonal and spatial soil respiration

Multiple regression analyses showed that the seasonal variation in soil respiration was primarily controlled by temperature, while soil water content had a weaker effect as well as a different influence on soil respiration depending on the time of the year (Table 4). The inclusion of the organic layer thickness parameter overrode the influence of both distance and fine root biomass in the multiple regression analyses, as these two parameters showed a high degree of autocorrelation with the organic layer thickness (data not shown). Bulk density in the top mineral layer showed a negative coefficient in the multiple regressions analyses that revealed the importance of porosity influencing the production and transport of CO_2 within the soil (Skopp et al. 1990; Fang and Moncrieff 1999). Overall, and allowing for the modest, though significant contribution made by the organic carbon concentration in the mineral soil, the multiple linear regression model allowed explaining 54% of total variance of soil respiration over the different stand ages for the entire year (Table 4). Other studies using similar parameters have produced models that explained total variance of soil respiration around the same order of magnitude as ours (Scott-Denton et al. 2003; Wiseman and Seiler 2004). The inclusion of other variables such as microbial biomass and soil chemical properties may improve the predictability of our model to explain total variance in soil respiration. However, we did not attempt to make use of those variables given our focus in using easily determinable parameters to explain such variability. Moreover, it has also been reported that the effect of each of the later factors pose on soil respiration may not be individually explained because they co-vary with soil organic matter and root respiration, major sources for soil respiration (Xu and Qi 2001). This argument further highlights the importance of organic layer thickness as one of the main determinants of soil respiration variability. Nonetheless, its importance may be dependant on having a significant proportion of total fine root biomass concentrated in this most superficial layer.

This study shows that the adoption of an adequate sampling strategy, and the determination of some key environmental variables may help to explain a large proportion of total variation of soil respiration over the entire rotation length of afforested ecosystems. Findings presented here may apply to a general context of afforestation carried out with commercial forestry species in temperate ecosystems; except for the case of the spatial variability of soil respiration. Such variability may be quite different in stands that have not full canopy closure, and in soils with very heterogeneous structural properties (i.e. podzols). Therefore, research over broader geographical areas and on different ecosystems is required to further assess the significance of the results presented here.

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